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BEHAVIORAL RESPONSES OF OCEANIC ZOOPLANKTON TO SIMULATED BIOLUMINESCENCE

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ABSTRACT

A defensive function often has been suggested for the bioluminescence of dinoflagellates and copepods, but there is only limited experimental evidence. Using closed circuit television equipment and infrared illumination we have recorded the behavioral responses of planktonic copepods, ostracods, polychaetes, chaetognaths, and euphausiids to simulated bioluminescent flashes. The swimming patterns of these organisms were then quantified using a video-computer system for motion analysis (the Bugwatcher). The photophobic response exhibited by certain copepod species in response to simulated dinoflagellate flashes, as well as the lack of response by several potential predators on copepods to their simulated bioluminescence, provide new insight into the roles of bioluminescence in plankton ecology. Comparison of the responses of the non-bioluminescent copepod *Calanus finmarchicus* and the bioluminescent copepod *Metridia longa* to simulated copepod bioluminescence show that *Metridia* is much more responsive than *Calanus*. This suggests that bioluminescence in *Metridia* may be recognized as a warning signal by conspecifics in addition to serving as a defense against predation.

INTRODUCTION

Most of the bioluminescence observed in the epipelagic zone is attributed to dinoflagellates and planktonic crustaceans such as copepods, ostracods, and euphausiids (Tett and Kelly, 1973; Swift *et al.*, 1983). Although the physical characteristics of the bioluminescence of these plankters has been carefully studied in several instances (*e.g.*, Harvey *et al.*, 1957; Eckert, 1967; Biggley *et al.*, 1969; Swift *et al.*, 1973; Widder *et al.*, 1983) there has been relatively little experimental work investigating the adaptive value of bioluminescence to planktonic organisms. Dinoflagellate bioluminescence has received the most attention, and the results of several studies provide evidence to support the hypothesis that dinoflagellates bioluminescence functions as a defense against nocturnal grazers such as copepods (Esaias and Curl, 1972; White, 1979; Buskey and Swift, 1983; Buskey *et al.*, 1983). Experimental studies also have suggested a defensive role for copepod bioluminescence (David and Conover, 1961).

One problem with studies of the behavior of planktonic bioluminescent organisms is that their bioluminescence is often photoinhibited at even low ambient light levels, making direct observation of behavioral interactions difficult or impossible. Another problem is that the behavioral interactions among zooplankters that lead to bioluminescent displays (*e.g.*, predator-prey interactions) are often low-frequency events and thus only rarely observed. We have overcome these problems by using infrared illumination to record on videotape the behavior of various planktonic organisms in darkness and by using an artificial light source to simulate the

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bioluminescent emissions of dinoflagellates and copepods. The responses of a variety of zooplankton species to bioluminescent flashes were observed and quantified using this technique, and this information was used to provide new evidence for the proposed roles of bioluminescence in zooplankton ecology.

Materials and Methods

Live zooplankton samples were taken in the vicinity of Iceland aboard the R/V Endeavor during cruise EN-103 in July 1983. Oblique tows were taken with 333 or 202 μm mesh plankton nets towed between the surface and *ca.* 100 m depth. A ship speed of <1 knot was maintained during these tows to reduce injury to the zooplankters. Upon recovery the contents of the cod ends of the nets were immediately diluted into one gallon glass jars with sea water at ambient temperature. From this container individuals of the plankton species chosen for study were then captured with a large bore pipette and transferred to 11 cm diameter Carolina culture dishes containing filtered sea water. These organisms were then observed under a dissecting microscope to check species identifications and to inspect for injury. Specimens showing signs of injury (*e.g.,* broken setae) were not used. Specimens were then held in incubators at ambient temperature for 12–24 hours before experimentation.

To test the effects of simulated bioluminescent flashes on the swimming behavior of the various zooplankton species collected, bioluminescent flashes were simulated using a diffuse horizontal light beam from a high intensity tungsten lamp passed through a 480 nm narrow band interference filter (10 nm half band width). Light intensity was adjusted using neutral density filters and by controlling lamp current (Oriel Model 6329 controller). Flash duration was adjusted by passing the light beam through a shutter with a Uniblitz model 310 controller, and photon flux was measured with a LICOR model 158A light sensor with quantum probe.

A flash of 480 nm blue light for 60 ms at an intensity of *ca.* 2 $\mu E \cdot m^{-2} \cdot s^{-1}$ was used to simulate dinoflagellate bioluminescence (Buskey and Swift, 1983). This flash approximates the light flux per unit area through the surface of a bioluminescent dinoflagellate (Seliger *et al.,* in prep.) and thus represents the maximum light dose that would be received by direct contact of a flashing dinoflagellate with a copepod eye. Copepod bioluminescent flashes are composed of light of similar spectral composition and intensity as in dinoflagellates (David and Conover, 1961; Herring, 1983; Widder *et al.,* 1983) but their light emission lasts considerably longer. The duration of bioluminescent displays by copepods are reported to range from 0.1 s to one minute or more (David and Conover, 1961; Clarke *et al.,* 1962; Barnes and Case, 1972) and seem to be highly dependent on the method of stimulation. When stimulated either by electrical shock (David and Conover, 1961; Clarke *et al.,* 1962; Barnes and Case, 1972) or by placing the animals on filter paper and removing the water (Clarke *et al.,* 1962), copepods produce considerably longer bioluminescent emissions than those produced by mechanical stimulation via a stirring rod (Barnes and Case, 1972; Swift *et al.,* in prep). Mechanical stimulation is most similar to the stimuli which normally induce bioluminescence in nature (*e.g.,* attempted capture by predators). Copepod bioluminescence is characterized by a rapid rise in intensity, a slower decay and a dim afterglow occasionally lingering for a period of up to a minute, but with >90 percent of light production in less than 1 s. Since this intensity pattern cannot be duplicated with our electronic shutter, a constant intensity flash of 600 ms duration was used to simulate copepod bioluminescence.

All experiments were performed on board ship in a darkened room. A closed

circuit television system was used to monitor and record swimming behavior of the zooplankters. Darkfield substage illumination, passed through an infrared transmitting filter (Kodak Safelight Filter No. 11), provided light for a Cohu 4400 television camera with a macro lens. Movement was monitored from above in the horizontal plane.

Four hours before video recording each experiment, organisms were transferred to 10 × 10 × 5 cm lucite chambers. From 1 to 5 individuals were placed in each chamber, depending on their size and activity level. These chambers had silicon rubber gaskets on their lids which allowed the chambers to be completely filled with sea water and sealed shut. The absence of air in the cuvette almost completely eliminated passive movement of the animals within the chamber caused by movements of the ship. Reported respiration rates for copepods (Vidal, 1980) and euphausiids (Mauchline, 1980) indicate that oxygen concentrations within the cuvettes should be depleted by less than five percent over the course of the experiments. The sealed chambers were placed in incubators at ambient temperatures (*ca.* 2–6°C) in complete darkness. Just prior to video recording, the experimental chambers were removed from the incubator and placed in a water bath to reduce changes in water temperature during the *ca.* 5 min video recording session. To ensure that the organisms were isolated from extraneous light produced by the experimental equipment, samples were placed in an opaque enclosure, with openings for the video camera, substage illumination, and horizontal light source.

In a typical experiment, the swimming behavior of the organisms was videotaped for a period of two minutes in the absence of simulated bioluminescence, and then for two minutes with light flashes introduced through the side of the chamber at five-second intervals. This experimental design allowed paired comparisons using Student's *t*-test of the swimming behavior of the same group of organisms. The paired comparison design is extremely useful for investigations of behavioral parameters since measured values can vary considerably even between individuals from the same population. To avoid recording interactions of the zooplankton with the side walls of the cuvette, only the central area (*ca.* 8 × 8 cm) was included in the field of view of the video camera.

After the cruise, videotapes of copepod swimming behavior were played back through a video-to-digital processor, the "Bugwatcher" (Wilson and Greaves, 1979), and the location of the digitized outline of each organism in the video field was input to a Data General Eclipse S120 computer at a rate of 10 frames $\cdot s^{-1}$ for organisms with slow or consistent swimming speeds (euphausiids, polychaetes and chaetognaths) or at a rate of 15 frames $\cdot s^{-1}$ for organisms with more rapid or variable swimming behavior (copepods and ostracods). The mean swimming speed was computed from the digitized paths of all organisms. The number of swimming speed bursts was determined by counting bursts that exceeded a threshold of 15 mm $\cdot s^{-1}$. Since frame by frame observation of videotapes revealed that these swimming speed bursts sometimes occurred in less than a single video frame (60 frames $\cdot s^{-1}$), the measured speed of these bursts based on a sampling rate of 15 frames $\cdot s^{-1}$ is at most ¼ of the true speed. In some cases, swimming speed bursts were so dramatic that the organisms jumped out of the field of view of the video camera (which included *ca.* 65% of the cuvette). Since speed bursts could not be measured by the computer in these cases, videotapes were also visually monitored to count the number of speed bursts when responses were too extreme to be quantified by computer.

The turning behavior of the organisms in the horizontal plane of observation were quantified as rate of change of direction and net to gross displacement ratio.

Rate of change of direction is simply the turning rate measured in degrees per second. The tendency of organisms to remain within an area by changing their turning behavior is indicated by the net to gross displacement ratios (NGDR) of their paths of travel. This measure is the ratio of the linear distance between starting point and ending point of the path (net displacement) to the total distance traveled for each path (gross displacement). Thus an increase in NGDR indicates a more linear swimming path, and a decrease in NGDR indicates a less linear, more circuitous swimming path. Direction of travel measures the angle between each segment of the path (for each 1/10 or 1/15 s) and the light source (0°). Distributions of direction of travel are calculated as percent distribution within each of twelve 30° arcs. These distributions of direction of travel are compared, using a Chi-square test, with a theoretical uniform distribution of direction of travel (Batschelet, 1965).

Results

The most commonly observed behavioral response of copepods to simulated dinoflagellate flashes are characterized by a sharp increase in swimming speed a few ms after the beginning of the flash (Fig. 1). Sometimes swimming speed bursts are preceded by turning behavior. We refer to all the responses to rapid changes in light intensity which elicit a transient alteration in the activity of the organism (*e.g.*, a burst of swimming speed) as photophobic responses (*sensu* Diehn *et al.*, 1977). The responses of the copepods tested in this study are similar to those previously observed in the estuarine copepod *Acartia hudsonica* exposed to both natural and simulated dinoflagellate bioluminescence (Buskey and Swift, 1983; Buskey *et al.*, 1983). The major difference between present and previous results was that the photophobic responses observed on this cruise were more intense than any previously recorded.

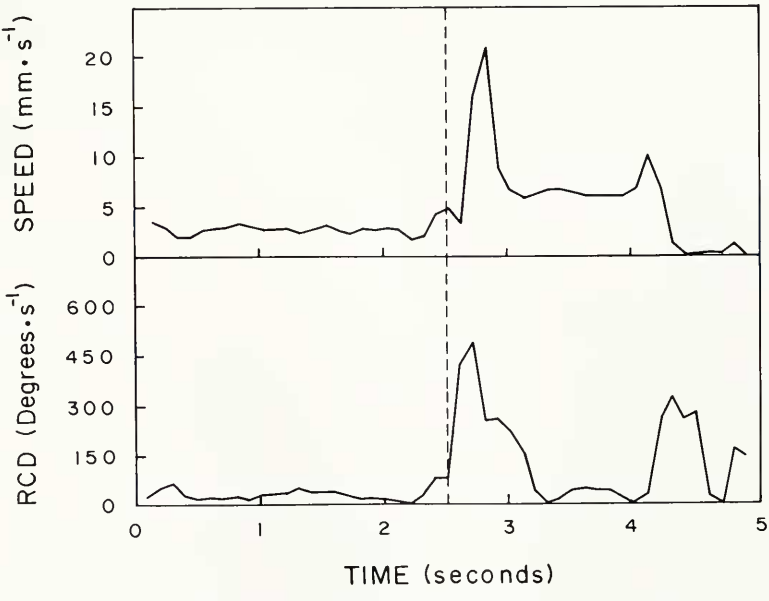

FIGURE 1. Record of swimming speed and the rate of change of direction (RCD) over time for a single *Calanus finmarchicus* exposed to a simulated bioluminescent flash (475 nm blue light for 60 ms duration at an intensity of 2 $\mu E \cdot m^{-2} \cdot s^{-1}$): the dashed line indicates the time of the flash.

The effects of simulated bioluminescence on the swimming behavior of a variety of copepod species (Table I) indicated strong photophobic responses and increased average swimming speeds for four of the six copepod species tested (*Calanus finmarchicus, Metridia longa, Metridia lucens, Temora longicornis*). Three of these

TABLE I

Responses of oceanic zooplankton to simulated bioluminescent flashes (475 nm peak emission, 60 ms duration, 2.0 $\mu E \cdot m^{-2} \cdot s^{-1}$ intensity)[a]

Species		Percent response[b]	Mean speed ($mm \cdot s^{-1}$)	Bursts/ min[c]	NGDR[d]
Calanus finmarchicus	C	80	2.02 (0.80)*	2.1 (2.6)*	0.41 (0.04)*
	E		4.98	10.3	0.71
Calanus hyperboreus	C	16	1.14 (0.18)	1.3 (0.9)	0.32 (0.05)
	E		1.31	1.8	0.36
Euchaeta norvegica	C	0	1.29 (0.18)	0.6 (0.8)	0.34 (0.03)
	E		1.12	0.2	0.39
Metridia longa	C	58	5.65 (0.48)*	0.7 (4.1)*	0.53 (0.03)*
	E		7.02	18.3	0.81
Metridia lucens	C	64	4.13 (1.09)*	2.7 (3.6)*	0.45 (0.06)*
	E		8.47	14.3	0.69
Temora longicornis	C	86	2.68 (0.83)*	0.5 (2.7)*	0.79 (0.03)
	E		6.05	15.9	0.75
Meganyctiphanes norvegica	C	0	4.71 (1.61)	0	0.41 (0.07)
	E		4.11	0	0.35
Conchoecia borealis	C	0	20.6 (2.4)*	1.6 (2.1)	0.84 (0.04)*
	E		29.9	3.9	0.42
Eukrohnia hamata	C	0	0.95 (0.61)	0	0.31 (0.11)
	E		0.88	0	0.42
Tomopteris septendrionalis	C	43	12.7 (3.5)	0 (2.1)*	0.61 (0.08)
	E		18.3	4.9	0.54

[a] Grand means for 10 groups of 1 to 5 organisms exposed to no light flash (C) and to flashes of blue light at 5 s intervals (E). The estimated standard error of the mean difference is given in parentheses. Significant differences are designated with an asterisk (Student's *t*-test with paired comparison design, $\alpha = 0.05$).

[b] The proportion of zooplankton responding to simulated bioluminescent flashes (Percent response) is based on visual monitoring of videotaped experiments.

[c] The number of swimming speed bursts for each experimental trial (Bursts) was normalized by dividing by the total number of minutes that zooplankton tracks were observed during the 2 minute video recording. Speed bursts had peaks >15 $mm \cdot s^{-1}$ for copepods, >30 $mm \cdot s^{-1}$ for *Tomopteris*, and >50 $mm \cdot s^{-1}$ for *Conchoecia*.

[d] Net to Gross Displacement Ratio.

four species (except *T. longicornis*) also showed a significant tendency to swim in straighter paths (increased NGDR), although *M. longa* and *M. lucens* exhibited rapid spiralling behavior while swimming in what was otherwise an essentially straight path. *Calanus hyperboreus* exhibited an occasional weak photophobic response but showed no significant changes in average swimming speed in the presence of simulated bioluminescence. *Euchaeta norvegica* showed no evidence of a photophobic response or other change in swimming speed. Despite the absence of strong photophobic responses, both *C. hyperboreus* and *E. norvegica* were occasionally observed to make "grasping" motions with their feeding appendages immediately after simulated bioluminescent flashes.

The paths of copepods exhibiting a photophobic response to the first light flash were pooled and analyzed separately from the paths of copepods not responding to the light for each species (see Table I for percent of animals responding). No significant difference was found between direction of travel distributions during the 1 s intervals before and after the flash (Chi-square test, $\alpha = 0.05$). This lack of difference suggests that the orientation of copepods with respect to the light source prior to the flash does not influence the frequency of response, nor does there seem to be a tendency for copepods responding to the flash to move preferentially toward or away from the light source immediately after the flash. Since bioluminescence in both dinoflagellates and copepods is stimulated by mechanical disturbances, potential predators and their prey should often be in direct contact when a bioluminescent flash is stimulated. Any subsequent photophobic response would tend to separate the predator and its prey, regardless of their direction of travel.

The responses of several other zooplankton species to simulated bioluminescence were also tested. Neither the euphausiid *Meganyctiphanes norvegica* nor the chaetognath *Eukrohnia hamata* showed any behavioral responses to simulated bioluminescence (Table I). The ostracod *Conchoecia borealis* exhibited no distinct photophobic response, but showed a general increase in swimming speed in the presence of simulated bioluminescence (Table I, Fig. 2) and a significant decrease in NGDR (Table I). These changes in behavior were the result of a rapid looping swimming pattern in the presence of simulated bioluminescence. In contrast, the planktonic polychaete *Tomopteris septendrionalis* showed a photophobic response consisting of a sharp turn followed by a rapid increase in swimming speed (Fig. 3) that was quite similar to the response in copepods (see Fig. 1).

More extensive tests, including the effects of changing flash color, intensity, and duration on photic responses were made with two common copepod species, *Calanus finmarchicus* (which is not bioluminescent) and *Metridia longa* (which is bioluminescent). The wavelength of light was varied to determine the wavelengths of greatest sensitivity for the photophobic responses of *Calanus finmarchicus* and *Metridia longa* (60 ms duration, 0.2 $\mu E \cdot m^{-2} \cdot s^{-1}$ intensity). Both species showed strong photophobic responses over a range of wavelengths between approximately 460–560 nm (Fig. 4). At this intensity (which represents *ca.* 10% of that given off by a bioluminescent dinoflagellate) the reactions of the copepods were so strong that it was impossible to define a narrower range of maximum sensitivity based on this photophobic response.

Varying the intensity of blue 60 ms flashes indicated that a strong photophobic response still occurs for copepods exposed to light intensities as low as 0.002 $\mu E \cdot m^{-2} \cdot s^{-1}$ (Table II). Lower light intensities were not used since our light sensor was not sensitive enough to measure light in this intensity range. At all four intensities tested there was a significant increase in average swimming speed, number of bursts in swimming speed, and NGDR for copepods exposed to simulated

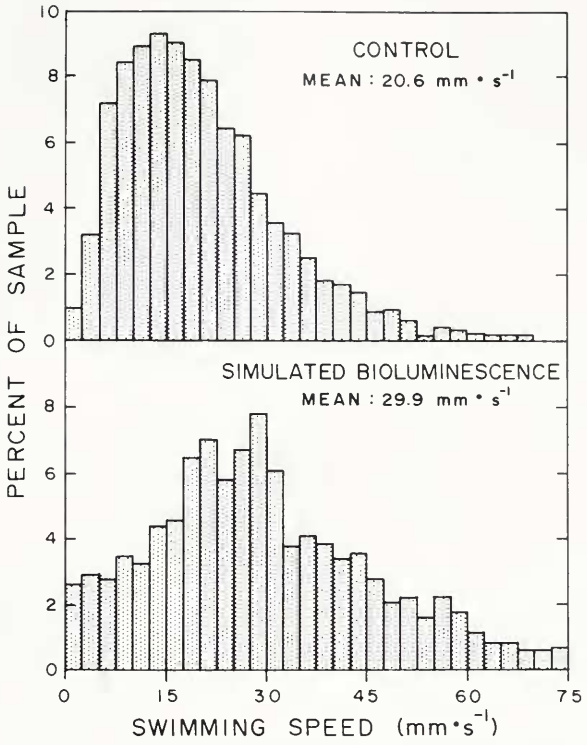

FIGURE 2. Distribution of swimming speeds for the ostracod *Conchoecia borealis* in complete darkness (top) and with a simulated bioluminescent flash (475 nm, 60 ms duration, 2 $\mu E \cdot m^{-2} \cdot s^{-1}$ intensity) presented every 5 s (bottom). These distributions are based on the pooled results from trials on 10 groups of ostracods with *ca.* 5 ostracods per trial. The mean is based on the total number of measurements of swimming speed made as the ostracods swam through the field of observation.

bioluminescent flashes compared to those under control conditions ($\alpha = 0.05$, Student's *t*-test with paired comparison design).

No effect of flash duration was found for the response of *Calanus finmarchicus* when the copepod was exposed to either 60 or 600 ms flashes. These responses were most easily compared as percent of copepods responding to the light flash (Table III). In contrast, *Metridia longa* showed a significantly greater percent response to 600 ms flashes than to 60 ms flashes at all intensities tested. By comparing the response of copepods to longer flashes at a given intensity *versus* shorter flashes at a higher intensity, it is also apparent that the difference in response to short and long flashes was not simply a function of total light dose. A 600 ms flash of 0.02 $\mu E \cdot m^{-2} \cdot s^{-1}$ intensity delivers the same total light dose as a 60 ms flash of 0.2 $\mu E \cdot m^{-2} \cdot s^{-1}$ intensity, yet the 600 ms flash still resulted in a greater percent response by *Metridia longa*.

DISCUSSION

One of the most commonly suggested functions of the bioluminescence of dinoflagellates and copepods is as a deterrent against nocturnal predation (Tett and Kelly, 1973; Buck, 1978; Porter and Porter, 1979; Morin, 1983; Young, 1983). All

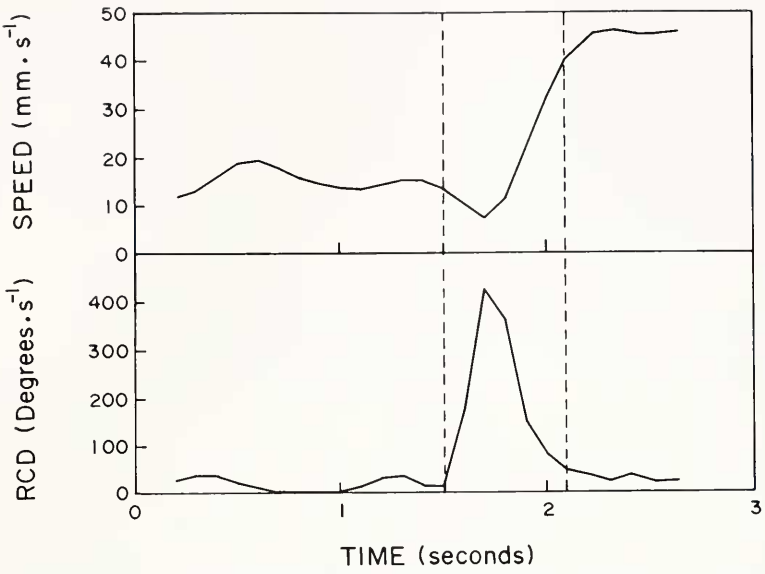

FIGURE 3. Record of swimming speed and rate of change of direction for a single *Tomopteris septendrionalis* exposed to a simulated bioluminescent flash (475 nm blue light for 60 ms duration at an intensity of 2 $\mu E \cdot m^{-2} \cdot s^{-1}$): the dashed lines indicate the beginning and end of the flash.

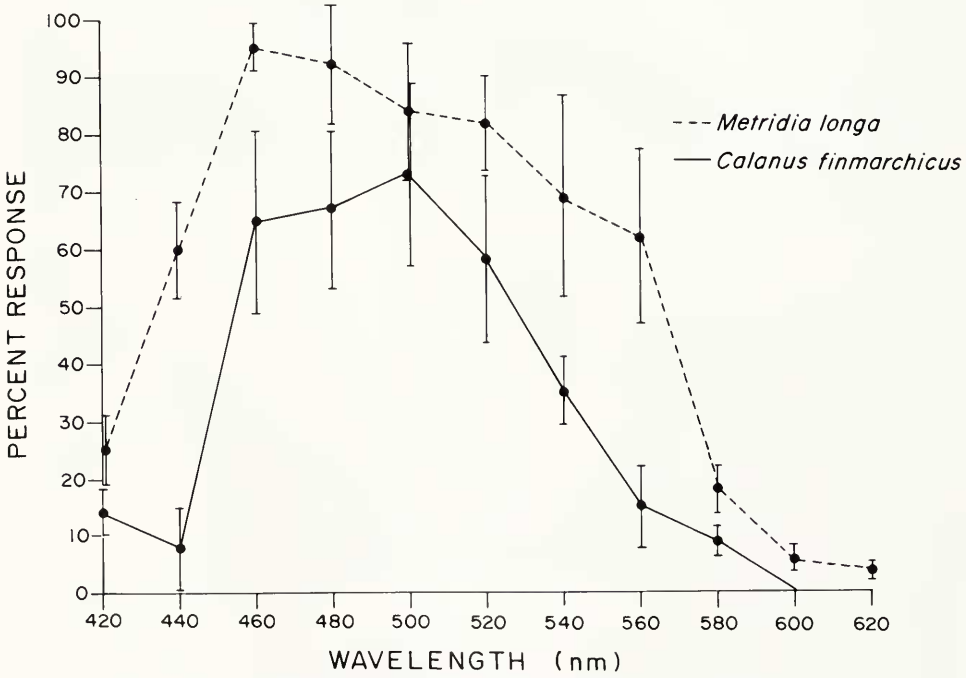

FIGURE 4. Effects of varying light color on the proportion of *Calanus finmarchicus* (solid line) and *Metridia longa* (dashed line) responding to simulated bioluminescent flashes (60 ms duration, 0.2 $\mu E \cdot m^{-2} \cdot s^{-1}$ intensity) with a burst of swimming speed. Vertical bars indicate the standard error of the mean value, based on 5 trials at each intensity with *ca.* 5 copepods per trial.

TABLE II

Parameters describing swimming behavior for Calanus finmarchicus *and* Metridia longa *exposed to simulated dinoflagellate flashes at different intensities*[a]

Intensity ($\mu E \cdot m^{-2} \cdot s^{-1}$)		Mean speed $mm \cdot s^{-1}$	Bursts/ min	NGDR
Calanus finmarchicus				
2.0	C	2.02	2.1	0.41
		(0.80)*	(2.6)*	(0.04)*
	E	4.98	10.3	0.71
0.2	C	1.98	3.6	0.34
		(0.53)*	(1.7)*	(0.09)*
	E	3.68	8.5	0.62
0.02	C	2.45	6.3	0.39
		(0.56)*	(1.1)*	(0.06)*
	E	5.81	13.7	0.64
0.002	C	1.83	2.8	0.37
		(0.88)*	(1.4)*	(0.07)*
	E	4.35	9.7	0.68
Metridia longa				
2.0	C	5.65	0.7	0.53
		(0.48)*	(4.1)*	(0.03)*
	E	7.02	18.3	0.81
0.2	C	4.51	1.5	0.47
		(1.03)*	(3.8)*	(0.04)*
	E	8.12	13.9	0.64
0.02	C	5.40	2.1	0.66
		(0.87)*	(2.7)*	(0.06)*
	E	9.14	14.2	0.85
0.002	C	4.21	1.7	0.52
		(0.39)*	(2.8)*	(0.04)*
	E	7.45	11.9	0.78

[a] Numbers are grand means for 10 groups of 5 copepods exposed to no light flash (C) and to flashes of blue light (E) (wavelength at peak emission 475 nm, duration 60 ms). The estimated standard error of the mean difference is given in parentheses. Significant differences are designated with an asterisk (Student's *t*-test with paired sample design, $\alpha = 0.05$).

the calanoid copepods we tested that were potential grazers on dinoflagellates responded to simulated dinoflagellate flashes with a photophobic response (Table I). These include species considered to be mainly herbivorous such as *Calanus finmarchicus* (Conover, 1960; Anraku and Omori, 1963; Gauld, 1966) and other copepod species considered to be omnivorous such as *Calanus hyperboreus* (Conover, 1966), *Temora longicornus* (Gauld, 1966), *Metridia lucens* (Haq, 1967; Harding, 1974), and *Metridia longa* (Haq, 1967). Our results provide further support for the hypothesis that dinoflagellate bioluminescence acts to deter predation by nocturnal grazers such as copepods. The bioluminescent flash stimulated by contact between a copepod and a bioluminescent dinoflagellate should elicit a photophobic response in the copepod. This burst of swimming speed by the copepod will interrupt the

TABLE III

Effect of flash duration on percent startle response for the non-bioluminescent copepod Calanus finmarchicus *and the bioluminescent copepod* Metridia longa[a]

Intensity ($\mu E \cdot m^{-2} \cdot s^{-1}$)	*Calanus finmarchicus*		*Metridia longa*	
	60 ms	600 ms	60 ms	600 ms
2.0	80	65	58	96
0.2	76	69	69	97
0.02	63	72	62	98
0.002	50	67	45	92

[a] Responses of copepods to 60 and 600 ms flashes at each intensity, and the responses of copepods to 60 ms flashes at one intensity and 600 ms flashes at lower intensity (same total light dose) were compared using the Chi-square test for two independent samples. An asterisk indicates a significant difference at $\alpha = 0.05$. Sample size range: 35–54 copepods per intensity–duration treatment.

feeding behavior of the copepod (Rosenburg, 1980) and physically separate the copepod and dinoflagellate by a distance of several centimeters. *Calanus hyperboreus* only exhibited occasional photophobic responses to simulated dinoflagellate bioluminescence (Table I). It is unclear whether this reduced response compared to other omnivorous copepods was due to the physiological state of the copepods (*e.g.*, trauma associated with their capture or handling) or if the limited response indicates that *C. hyperboreus* is truly less susceptible to the bioluminescent defenses of dinoflagellates.

There have been several detailed studies of bioluminescent copepods (David and Conover, 1961; Clarke *et al.*, 1962; Barnes and Case, 1972) but only the study of David and Conover (1961) investigated the role of bioluminescence in copepod ecology experimentally. In their experiments the euphausiid *Meganyctiphanes norvegica* and *ca.* 10 bioluminescent copepods (*Metridia lucens*) were placed in a beaker in front of a photomultiplier tube in darkness. The number of multiple flash sequences corresponded well to the number of copepods consumed, and these multiple flashes were assumed to represent bioluminescence stimulated during capture and consumption of copepods. Since flashes were rarely recorded when *Metridia* was held separately or in the presence of non-predatory euphausiids or amphipods, single flashes were assumed to represent attempted captures and successful escapes. The results of David and Conover do not provide evidence that bioluminescence aided the escape of the *Metridia lucens* from *Meganyctiphanes norvegica*, however. Since bioluminescence is stimulated mechanically in copepods, bioluminescence should be produced during any attempted capture and subsequent handling of the copepods. Additional experimental evidence is needed to determine if the bioluminescent flash increases the probability of escape. The results of our study show no apparent change in the behavior of *M. norvegica* when exposed to simulated copepod bioluminescence (Table I). This lack of response by *M. norvegica* could be due to a number of experimental conditions (*i.e.*, confinement, shock from capture, etc.) so these results do not rule out a defensive role for bioluminescence in *M. norvegica-M. lucens* predator-prey interactions. However, the lack of response to simulated bioluminescence by three potential invertebrate predators on *Metridia*

(*Meganyctiphanes, Eukrohnia,* and *Euchaeta*) suggests that the proposed defensive function of bioluminescence in *Metridia* may have evolved instead for defense against visual predators such as planktivorous fish, or for some purpose other than defense. We have not yet tested the responses of fish to simulated bioluminescence.

Of the potential predators on copepods we tested, only *Tomopteris septendrionalis* responded to a simulated copepod flash with a sharp increase in swimming speed (Fig. 3, Table I). Thus bioluminescence of *Metridia* and other bioluminescent organisms could potentially serve as a deterent to predation by *Tomopteris,* although the extent to which this predation occurs in nature is unknown. Dales (1971) has suggested that bioluminescence in *Tomopteris* might serve as a mating signal. It seems unlikely that the photophobic response to a diffuse blue light flash that we observed for *Tomopteris* would represent an adaptation for mate location. The bioluminescent display produced by *Tomopteris* is quite different than that produced by *Metridia,* however, and a specific photic signal might be required to elicit mating behavior in *Tomopteris.* The peak wavelengths of light emission is between 560–580 nm for *Tomopteris septendrionalis* (Terio, 1960 cited in Dales, 1971) compared to a peak of *ca.* 480 nm for *Metridia lucens* (David and Conover, 1961). The occurrence and distribution of the light-producing rosette organs in the parapodia of *Tomopteris* varies between different *Tomopteris* species and thus could produce species specific patterns that might act as recognition signals for mating (Dales, 1971).

Ostracods of the genus *Conchoecia* are reported to feed mainly on dead crustaceans and small masses of detritus (Lochhead, 1968; Angel, 1970) and are probably not potential predators on either dinoflagellates or copepods. Therefore lack of a photophobic or "startle" response by *Conchoecia borealis* to simulated dinoflagellate and copepod bioluminescence observed in this study neither supports nor refutes a hypothetical defensive function of bioluminescence in these groups. The response of *C. borealis* to simulated bioluminescence was a general increase in swimming speed and a increased curvature of swimming paths (Table I). The adaptive value of this photokinetic response is not obvious, but perhaps these changes in behavior represent an avoidance response elicited when in the presence of high concentrations of bioluminescent dinoflagellates, whose luminescence might reveal the location of the ostracods to visual predators (Burkenroad, 1943). *C. borealis* is itself bioluminescent, and although the biochemistry of luminescence is well known in the Ostracoda, little is known about the ecology of their bioluminescence (Tett and Kelly, 1973). The secretion of bioluminescent clouds by ostracods in response to mechanical stimulation (Angel, 1968) suggests at least a defensive role for ostracod bioluminescence.

In this study a bioluminescent copepod (*Metridia longa*) was found to be more responsive to simulated copepod bioluminescence than to simulated dinoflagellate bioluminescence (Table III). No similar difference in responsiveness was found in either the non-bioluminescent copepod tested during this study (*Calanus finmarchicus*) or in the non-bioluminescent estuarine copepod tested in a previous study (*Acartia hudsonica,* Buskey and Swift, 1983). This difference suggests that the behavioral response of *Metridia longa* may have evolved by increasing its sensitivity to longer duration flashes such as those produced by conspecifics. This type of response could have potential adaptive value since long duration (>600 ms) bioluminescent signals from conspecifics could indicate an attack by a predator such as a euphausiid, since bioluminescence in copepods is stimulated primarily by interaction with predators (David and Conover, 1961).

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